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Paleoecological and microenvironmental aspects of the first European hominids inferred from the taphonomy of small mammals (Sima del Elefante, Sierra de Atapuerca, Spain)



Aspects paléoécologiques et microenvironnementaux des premiers hominidés européens, inférés à partir de la taphonomie de petits mammifères (Sima del Elefante, Sierra de Atapuerca, Espagne)

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ABSTRACT

Unit TE9 of the Sima del Elefante (Sierra de Atapuerca, Burgos, Spain), where the remains of *Homo* sp. have been discovered (1.2–1.3 Ma), is also a level rich in small mammals. The taphonomic study of these small vertebrates sheds light on the landscape that provided the setting for the activities of these early hominids and allows us to describe what the cave was like during the formation of the level. Small mammal predators identified in the study indicate that during this period the Sierra de Atapuerca was part of a large biome consisting of semi-open riparian forests with meadows nearby. Postdepositional alterations reveal that the production of fossils took place outside the cave, being transported inside by water currents. During the formation of TE9, the cave presented conditions of high humidity, which made it difficult for hominids to establish occupations inside, although these conditions became somewhat less severe in TE9c, the sublevel where human remains are found.

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R É S U M É

Le niveau TE9 de Sima del Elefante (Sierra de Atapuerca, Burgos, Espagne), où des restes d'*Homo* sp. ont été découverts (1,2–1,3 Ma), est également un niveau riche en petits mammifères. L'étude taphonomique de ces petits vertébrés met en lumière le paysage qui fournit le cadre des activités de ces premiers hominidés et permet de décrire comment était la grotte lors de la formation du niveau. Les prédateurs des petits mammifères identifiés dans l'étude indiquent que, pendant cette période, la Sierra de Atapuerca faisait partie d'un vaste biome composé de forêts riveraines semi-ouvertes et de prés. Des altérations postdépositionnelles révèlent que la production de fossiles a eu lieu hors de la grotte et que ceux-ci y

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ont été transportés par les cours d'eau. Pendant la formation du niveau TE9, l'humidité de la grotte était élevée, ce qui a rendu son occupation par les hominidés difficile. Ces conditions devinrent toutefois un peu moins sévères au TE9c, le sous-niveau où des restes humains ont été trouvés.

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1. Introduction

In addition to a large and rich archaeological and paleontological record, the Sima del Elefante site contains one of the oldest human fossils in Europe (Carbonell et al., 2008). The small mammal assemblages associated with the fossil human remains provide the best tool for ascertaining the paleoecological features of the sites where there were human activities during the Early Pleistocene of western Eurasia. In this paper, we present our contribution to this paleoenvironmental analysis by studying the taphonomy of the small mammal assemblages recovered from TE9 unit.

The site of Sima del Elefante is located in the karst system of the Sierra de Atapuerca, near Burgos (Spain) (Fig. 1A). The cave is filled with a stratigraphic succession 25 m thick and 15 m wide. The lower fill is the product of the massive entry of debris flow and alluvial sediments (Ortega et al., 2013). The exposed succession has been divided into 16 stratigraphic units (TE7–TE21) (Huguet et al., 2013) (Fig. 1B and C). The lower units (TE7–TE14), also known as the Lower Red Unit or TELRU, are rich in faunal remains, most of which are very well preserved, providing one of the best collections of fossil vertebrates from the Early Pleistocene in Europe (Blain et al., 2010; Carbonell et al., 2008; Cuenca-Bescós et al., 2010, 2013; García et al., 2008; *inter alia*). This faunal assemblage correlates units TE7 to TE14 with other Western-European localities that are biostratigraphically dated to a Late Villafranchian or Early Biharian age, localities such as Bagur 2, Fuentenueva 3, Barranco León D, Le Vallonnet, Les Valerots, among others. These Late Villafranchian localities are situated in the late Matuyama, pre-Jaramillo paleomagnetic zone, thus dating to around 1.5 to 1.2 Ma (Cuenca-Bescós et al., 2013). In unit TE9, four sublevels have been identified (TE9a, TE9b, TE9c and TE9d) (Fig. 1C). Of particular note in this unit is the high number of small vertebrate fossil remains (Table 1).

The paleomagnetic analysis shows a reverse polarity magnetization in level TE16 attributed to the Matuyama Chron (Parés et al., 2006), establishing a feasible timeline for levels TE7–TE16 framed between 1.3 and 0.78 Ma. Further, cosmogenic nuclide dating has placed level TE9c of Sima del Elefante at a burial age of 1.22 ± 0.16 Ma (Carbonell et al., 2008).

Noteworthy is that the lower levels from Sima del Elefante (TE7–TE14) represent one of the oldest and most continuous record of hominid activity in Europe. This is documented from the presence of stone tools and anthropogenic modifications in large mammal bones along the stratigraphic sequence, and especially from remains of *Homo* sp. in TE9c (Bermúdez de Castro et al., 2011; Carbonell et al., 2008; de Lombera-Hermida et al., 2015; Huguet et al., 2013; Lorenzo et al., 2014) (Fig. 1C).

Small mammals from archaeological sites have provided considerable information on environmental conditions during the Quaternary in Europe (Cuenca-Bescós et al., 2009, 2010, 2011, 2013; López-García et al., 2011, 2014; Popova, 2015; *inter alia*). However, paleoenvironmental reconstruction is not only a matter of applying what is known about modern ecology to interpreting past conditions. It is necessary to estimate the relationship between the animals under study and their environment, bearing in mind that the sample does not always correspond to the original association. In other words, one must identify the processes that have caused a bias in the sample studied in order to understand the original environment. This involves uncovering the taphonomic history of the sample: identifying the agent of accumulation and the depositional environment in which the remains accumulated. In the case of micromammals recovered from caves, the agent of accumulation is frequently associated with predation (Andrews, 1983, 1990; Chaline and Mein, 1979; Denys, 1986; Denys et al., 1987; Dodson and Wexlar, 1979; Jaeger, 1979; Korth, 1979; Kowalski, 1990; Kusmer, 1990; Mayhew, 1977; Mellet, 1974; *inter alia*). Thus, the main biases will concern the dietary preferences of the predator (opportunistic or selective), the extent and diversity of the hunting area, prey size and the damage to the prey remains caused by the predator. It is therefore essential to identify the predator by recognizing characteristic damage patterns and to establish the biases proper to individual predator species (Andrews, 1990). Furthermore, identification of the predator makes it possible to undertake a paleoecological assessment on the basis of its preferential habitat (Andrews, 1993, 1990; Denys, 1986).

The taphonomic study also includes a description of the modifications related to the processes characteristic of the depositional environment. Good examples are water flows, roots, trampling, weathering, etc. Sequencing of these processes enables us to ascertain the different sources of input, the depositional environment of the remains and the processes involved in the formation of unit TE9, in other words the taphonomic history of the association after its production.

The objectives of this study are to identify and describe the paleoenvironmental features of the Sierra de Atapuerca around 1.3 Ma on the basis of data extracted from the small mammals of unit TE9 of the site of Sima del Elefante. To this end, the predator or predators that produced the small mammal accumulations are identified. At the same time, surface modifications are used to determine the microenvironmental features of the cave, thus contributing to what is known about the karst taphosystem of the Sierra de Atapuerca.

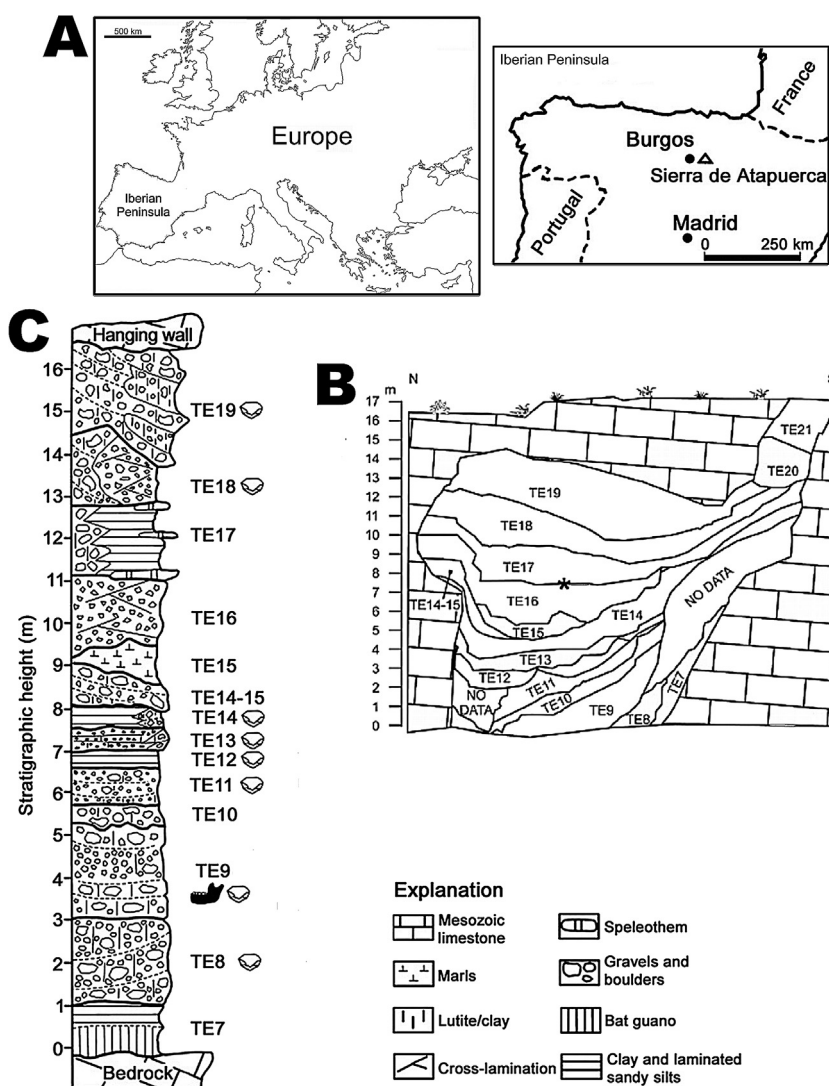


Fig. 1. A. Geographic context of the Sima del Elefante site. B. Stratigraphic section of Sima del Elefante (modified from Huguet et al., 2013). The asterisks mark the position of the Matuyama–Brunhes boundary. Heights are measured from the floor of the railway trench (Rodríguez et al., 2011). C. The synthetic column shows the different lithostratigraphic units visible in the central-north section. ☉ Lithic industry level. 🐼 Human remains level.

Fig. 1. A. Contexte géographique du site de Sima del Elefante. B. Section stratigraphique de Sima del Elefante (modifié d'après Huguet et al., 2013). Les astérisques marquent la position de la limite Matuyama–Brunhes. Les hauteurs sont mesurées à partir du fond de la tranchée du chemin de fer (Rodríguez et al., 2011). C. La colonne synthétique montre les diverses unités lithostratigraphiques visibles dans la partie centrale-nord. ☉ Niveau de l'industrie lithique. 🐼 Niveau des restes humains.

2. Materials and methods

This study includes an analysis of small mammal remains from 9 samples from sublevels TE9a, TE9b and TE9c. The process of microfossil recovery begins with the washing and screening of all the sediment obtained from the archaeo-paleontological excavation of the Sima del Elefante site. The washing is done with three superimposed sieves of decreasing wire mesh size (5 mm, 2 mm and 0.5 mm). Once the concentrate produced by the washing has been dried, the sorting takes place. Later, each of the remains is analyzed through a binocular magnifying glass (OPTECH SL Dual 6.5 ×–60 ×). For a detailed study of the remains and high-resolution photographs, a

variable-pressure environmental scanning electron microscope or ESEM (FEI QUANTA 600) is used under low-vacuum conditions, applying a high voltage (15 to 20 kV) and using secondary electron detectors (LFD detector) at the University Rovira i Virgili of Tarragona (Spain).

Given the large quantity of material we have available, we use selected samples from the same squares throughout the sequence TE9 always proportional to the excavated volume of sediment and the density of bone within it. From each of the samples all the remains are recorded, and a taphonomic analysis of the rodent and insectivore elements is performed. Lagomorphs are not included and will be the subject of a future taphonomic study. Order, family and species are identified using M_1 as a diagnostic element,

Table 1

Vertebrate species in unit TE9 of the Sima del Elefante site.

Tableau 1

Espèces vertébrées de l'unité TE9 du site de Sima del Elefante.

Taxons of level TE9 Sima del Elefante	
Primates (Carbonell et al., 2008; Bermúdez de Castro et al., 2011)	<i>Macaco</i> sp., <i>Homo</i> sp.
Carnivora (Rodríguez et al., 2011)	<i>Vulpes</i> cf. <i>alopecooides</i> , <i>Canis</i> sp. (<i>mosbachensis/arnensis</i>), <i>Lynx</i> cf. <i>issiodorensis</i> , cf. <i>Baranogale antiqua</i> , <i>Ursus dolinensis</i> , <i>Pannonictis nestii</i> , <i>Mustela palerminea</i> , <i>Panthera gombaszoegensis</i>
Artiodactyla (Rodríguez et al., 2011)	<i>Bison</i> cf. <i>voigtstedtensis</i> , <i>Cervidae</i> indet., <i>Dama</i> "nestii" <i>vallonnetensis</i> , <i>Sus scrofa</i> .
Perissodactyla (Rodríguez et al., 2011)	<i>Equus altidens</i>
Rodentia (Cuenca-Bescós et al., 2013)	<i>Allophaiomys lavocati</i> , <i>A. nutiensis</i> , <i>A. burgondiae</i> , <i>Pliomys</i> cf. <i>simplicior</i> , <i>Ungaromys</i> sp., <i>Arvicolajacobaeus</i> , <i>Castillomys rivas</i> , <i>Sciurus</i> sp., <i>Eliomys quercinus</i> , <i>Castorfiber</i> , <i>Apodemus</i> sp., <i>Microtus</i> sp., <i>Iberomys brecciensis</i> , <i>Microtus arvalis</i> , <i>Microtus agrestis</i> , <i>Arvicola</i> aff. <i>sapidus</i> , <i>Clethionomys</i> sp.
Eulipotyphla (Rofes and Cuenca-Bescós, 2013)	<i>Beremendia fissidens</i> , <i>Asoriculus gibberodon</i> , <i>Crociodura kornfeldi</i> , <i>Erinaceus</i> cf. <i>europaeus</i> , <i>Talpa</i> cf. <i>europaea</i> , <i>Sorex margaritodon</i> , <i>Sorex</i> sp.
Chiroptera (Cuenca-Bescós et al., 2013)	<i>Myotis</i> sp., <i>Rhinolophus</i> sp., <i>Miniopterus schreibersii</i>
Lagomorpha (de Marfà, 2009)	<i>Oryctolagus</i> cf. <i>giberti</i> , <i>Lepus</i> sp.
Aves (several orders) (Sánchez-Marco, 2004)	<i>Anas</i> sp., <i>Haliaeetus albicilla</i> , <i>Falco tinnunculus</i> , <i>Perdix palaeoperdix</i> , <i>Columba livia/oenas</i> , <i>Carduelis chloris</i> , <i>Acanthis flammea</i> , <i>Corvus antecorax</i> , <i>Pyrrhocorax pyrrhocorax</i> , <i>Corvus corax</i> s. <i>frugilegus</i> , <i>Lagopus mutus</i> , <i>Phoenicurus ochruros</i> , <i>Turdus</i> sp., <i>Lymnocyptes minimus</i> , <i>Vanellus vanellus</i>
Chelonía (Blasco et al., 2011)	<i>Testudo hermanni</i> , <i>Emys</i> cf. <i>E. orbicularis</i>
Amphibia and Squamata (Blain et al., 2010)	<i>Salamandra salamandra</i> , <i>Triturus</i> cf. <i>marmoratus</i> , <i>Alytes obstetricans</i> , <i>Pelobates cultripes</i> , <i>Pelodytes punctatus</i> , <i>Bufo bufo</i> , <i>B. calamita</i> , <i>Hyla arborea</i> , <i>Rana</i> sp., <i>Lacerta</i> s.l., <i>Anguis fragilis</i> , <i>Natrix</i> cf. <i>natrix</i> , <i>Natrix</i> cf. <i>maura</i> , <i>Coronella</i> cf. <i>gironica</i> , <i>Vipera</i> sp.

but in the absence of this element a diagnostic cranial or postcranial element is used. The determinations are based on the works of Cuenca-Bescós et al. (1995, 2013), Laplana and Cuenca-Bescós (2000), Rofes and Cuenca-Bescós (2006, 2009a, 2009b, 2013). Moreover, the fossils were grouped using the minimum number of individuals (MNI) method, from each sublevel, by counting the best diagnostic element, taking into account, whenever possible, laterality.

For the taphonomic study of the remains, the systematic-descriptive method described by Andrews (1990) is used. Superficial alterations present in the small mammal remains are observed and described (the representation of skeletal elements, the breakage and the degree of digestion), allowing the intervention of the predators to be identified and recognized.

To understand and describe the representation of the elements, we use indicators of the relative abundance of the skeletal elements (Andrews, 1990) and of the proportions of the skeletal elements (postcrania/crania; femur + humerus/maxilla + mandible; radius + tibia/humerus + femur; following Andrews, 1990; Fernández-Jalvo and Andrews, 1992). Subsequently, the fractures and the digestion of the elements are analyzed differentially and specifically for the postcranial elements, maxilla, mandible, molars and incisors (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). Finally, the study is completed with an analysis of the postdepositional modifications present on the surface of the fossils. Whenever possible, these modifications are recorded taking into account the degree of alteration, although in the majority of cases only their presence or absence could be noted.

3. Results

The total number of fossils studied from TE9 of Sima del Elefante is 4784, with a total MNI of 491. TE9c is the sublevel

with the fewest remains and the lowest number of species (Tables 2 and 3). All the levels feature individuals belonging to the class Mammalia, especially the orders Rodentia and Eulipotyphla (Table 2). Among the rodents *Allophaiomys lavocati* stands out, as does *Talpa* cf. *T. europaea* within the order Eulipotyphla (Table 2).

Among the sublevels of TE9, there are similarities in the presence of species and the alterations. All the anatomical elements are present in each sublevel (Table 3). The relative abundance of the skeletal elements indicates that the average representation is 32.9%, with sublevel TE9b remarkable for its low average representation (25.3% of the remains expected for the MNI calculated). The ratios between postcranial and cranial elements show a predominance of cranial remains (Table 4). Notable is the preferential destruction of the distal elements of the legs (Table 4). The breakage of the elements in TE9 and the loss of teeth in maxillae and mandibles are high (Table 5). The TE9b assemblage, despite its low representation, shows slightly lower fracture rates than TE9c and TE9a, where the breakage is mostly heavy and extreme. Note, for example, that the molars in the samples from TE9b tend to be retained in their alveoli and that there are more complete postcranial elements and mandibles than in the other sublevels (Table 5).

In all the samples studied, there are elements of rodents and insectivores with signs of digestion (Fig. 2). The digestion in levels TE9c, TE9b and TE9a is similar and affects about 30% of the remains (Table 6). In all sublevels, the most frequent degree of alteration is light (Table 6), although it is noteworthy that heavy degrees are reached in incisors (and even extreme degrees in TE9b) and moderate degrees in molars and postcranial elements.

Regarding postdepositional alterations, there is abundant precipitation of manganese oxides in TE9, descending slightly in TE9c (Table 7). Alterations caused by water

Table 2

Minimum number of individuals of small mammals used for the taphonomic study in the TE9 sublevels.

Tableau 2

Nombre minimum d'individus de petits mammifères, utilisé pour l'étude taphonomique dans les sous-niveaux TE9.

Minimum number of individuals							
	TE9						
	TE9c		TE9b		TE9a		
	MNI	%	MNI	%	MNI	%	
Rodentia							
<i>Allophaiomys lavocati</i>	54	68.4	195	75	113	74.3	
<i>Arvicola jacobaeus</i>	1	1.3	5	1.9	2	1.3	
<i>Castillomys rivas</i>	11	13.9	25	9.6	10	6.6	
<i>Apodemus</i> sp.	0	0	0	0	2	1.3	
<i>Ungaromys</i> sp.	0	0	0	0	3	2	
Eulipotyphla							
<i>Talpa</i> cf. <i>europaea</i>	7	8.9	17	6.5	11	7.2	
<i>Erinaceus</i> cf. <i>europaeus</i>	1	1.3	1	0.4	0	0	
<i>Beremendia fissidens</i>	1	1.3	7	2.7	3	2	
<i>Sorex</i> sp.	1	1.3	4	1.5	4	2.6	
<i>Crociodura</i> sp.	3	3.8	6	2.3	4	2.6	
Total	79		260		152		

Table 3

Number of elements and relative abundance of the skeletal elements for sublevels TE9c, TE9b and TE9a.

Tableau 3

Nombre d'éléments et abondance relative d'éléments squelettiques dans les sous-niveaux TE9c, TE9b et TE9a.

Small mammals remains									
Skeletal elements	TE9								
	TE9c			TE9b			TE9a		
	n	%	Relative abundance	n	%	Relative abundance	n	%	Relative abundance
Maxilla	88	9.1	112.8	221	9.9	85	173	11	113.8
Mandible	132	13.7	84.6	331	14.8	63.7	189	12	62.2
Molar	193	20	20.6	737	32.9	23.6	441	27.9	24.2
Incisor	214	22.2	68.6	238	10.6	22.9	341	21.6	56.1
Zygomatic arch	18	1.9	11.5	11	0.5	2.1	12	0.8	3.9
Humerus	44	4.6	28.2	53	2.4	10.2	47	3	15.5
Radius	5	0.5	3.2	14	0.6	2.7	6	0.4	2
Ulna	13	1.3	8.3	20	0.9	3.8	16	1	5.3
Femur	47	4.9	30.1	51	2.3	9.8	33	2.1	10.9
Tibia	25	2.6	16	30	1.3	5.8	41	2.6	13.5
Pelvis/Scapula	9	0.9	–	32	1.4	–	22	1.4	–
Vertebra	66	6.8	–	255	11.4	–	82	5.2	–
Rib	3	0.3	–	42	1.9	–	25	1.6	–
Autopodial	23	2.4	–	39	1.7	–	54	3.4	–
Undetermined	84	8.7	–	167	7.5	–	97	6.1	–
Total	964			2241			1579		

Table 4

Index of element proportions for the small mammals of level TE9. Results in %.

Tableau 4

Indice des proportions d'éléments pour les petits mammifères du niveau TE9. Résultats en %.

Element proportions	TE9		
	TE9c	TE9b	TE9a
	Postcrania/crania	0.7	0.3
Femur+humerus/maxilla+mandible	0.4	0.2	0.2
Radius+tibia/humerus+ femur	0.3	0.4	0.6

abrasion as well as by changes in humidity and dryness have been recorded, including concretions (mostly in TE9c), cracking and fractures produced by fallen rocks and sediment pressure. The differences between the three sublevels are present in alterations affecting less than 2% of the remains (dissolution, chemical corrosion, weathering and grooves caused by roots). It is worth highlighting that only in TE9b have we recorded cracking and exfoliations related to subaerial exposure and only in TE9a are there alterations caused by roots (Table 7).

4. Discussion

The results of the taphonomic study of the small mammal remains from unit TE9 of Sima del Elefante shed

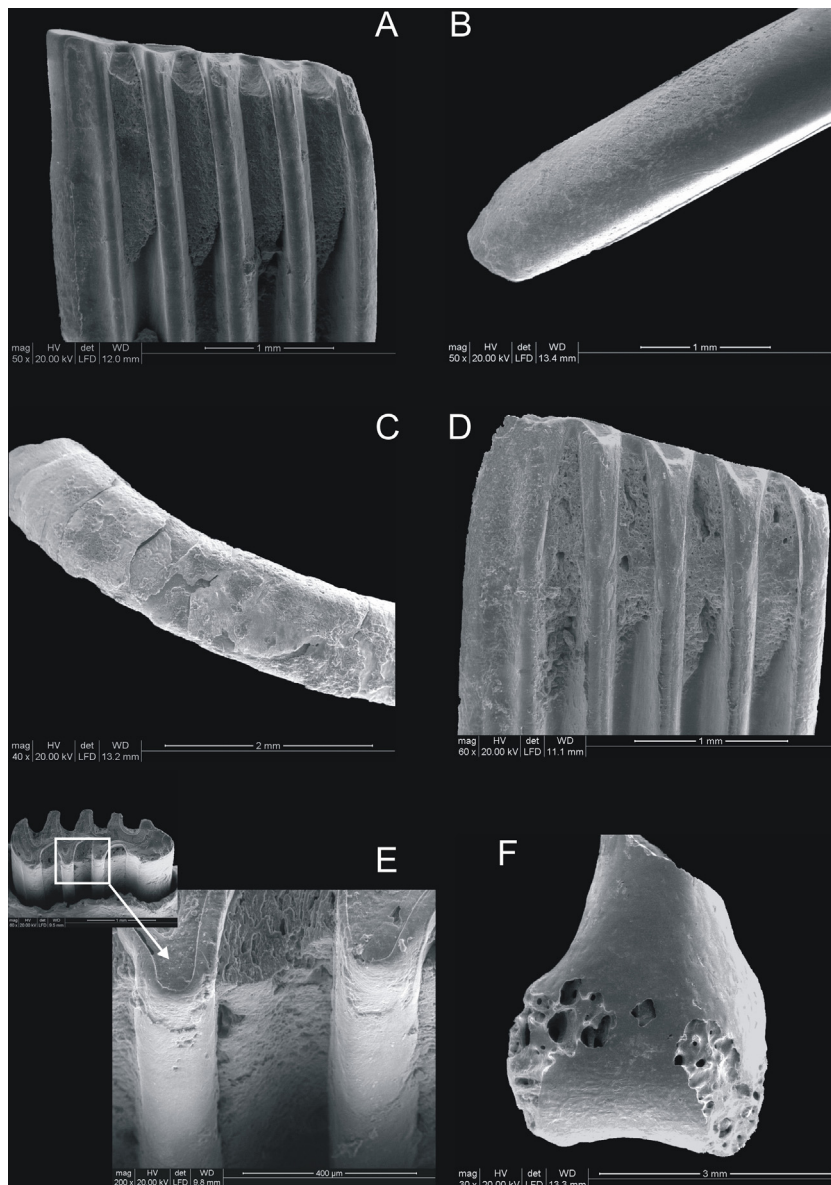


Fig. 2. Digestion in small mammal elements from sublevels TE9. TE9c: A. Moderate digestion in *M*₁ *Allophaiomys lavocati*. B. Inferior incisor of rodent with light digestion; TE9b: C. Digestion in heavy degree of rodent incisor. D. *A. lavocati* *M*₁ with moderate digestion. TE9a: E. Situation and detail of the vertices of molars affected by light digestion. F. Digestion in femur of *Talpa cf. europaea*.

Fig. 2. Digestion sur des éléments de petits mammifères des sous-niveaux TE9. TE9c : A. Digestion modérée sur une *M*₁ *Allophaiomys lavocati*. B. Incisive inférieure de rongeur à digestion légère ; TE9b : C. Digestion de haut degré sur une incisive de rongeur. D. *M*₁ d'*A. lavocati* à digestion modérée. TE9a : E. Situation et détail du sommet des molaires affectées par une digestion légère. F. Digestion sur un fémur de *Talpa cf. europaea*.

valuable light on the landscape of the Sierra de Atapuerca and on the depositional microenvironment from 1.2–1.3 Ma.

In the light of the alterations caused by digestion, it has been estimated that the origin of the small mammal accumulations is related to the biological activity of predators. While these alterations appear to be similar among the three sublevels, detailed analysis reveals certain differences. It is thus observed that the small mammal fossils

from TE9b show less fracturing but at the same time higher degrees of digestion than those from TE9c and TE9a, which are more similar to one another.

In TE9c and TE9a, the percentage of molars and incisors affected by digestion is greater than expected for a category 1 predator of modification (0–6% molars, 8–30% incisors), but slightly lower than expected for a predator category 2 (11–22% molars, 48–70% incisors) (Andrews, 1990). However the percentage of postcranial digested (25–50%) and

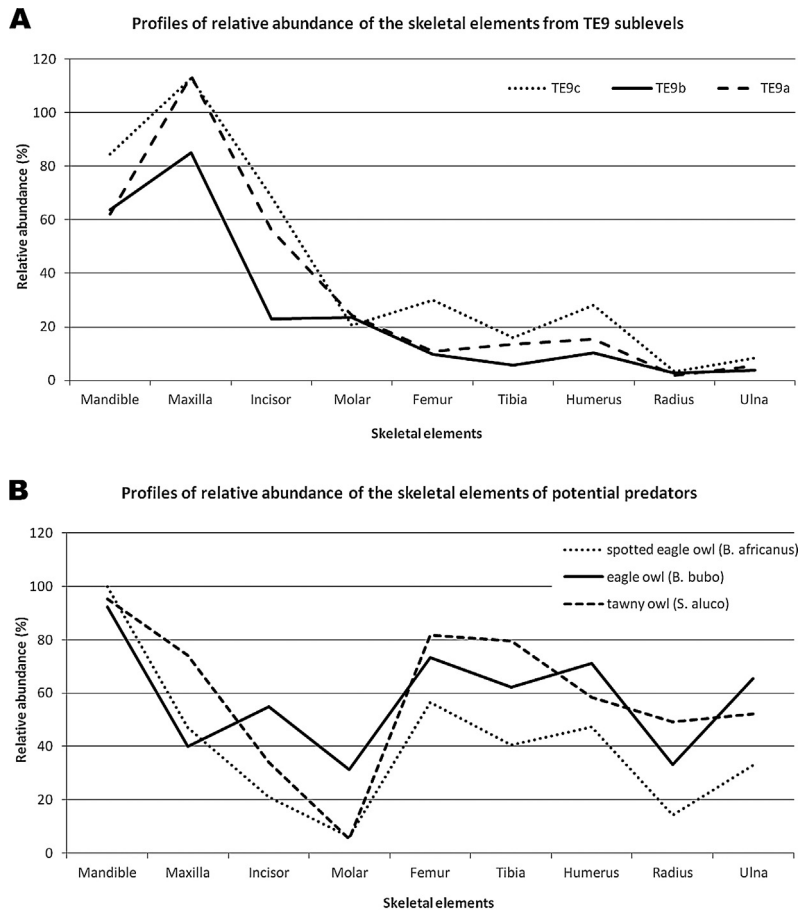


Fig. 3. Profiles of relative abundance of the small mammal skeletal elements from sublevels TE9c, TE9b and TE9a of Sima del Elefante site (A) and potential predators (B).

Fig. 3. Profils de l'abondance relative des éléments des petits mammifères des sous-niveaux TE9c, TE9b et TE9a du site de Sima del Elefante (A) et de possibles prédateurs (B).

degrees of alteration achieved in molars and incisors (moderate and heavy digestion) could correspond to that exerted by a category 2 predator of modification (Andrews, 1990). Among the predators in this category are the spotted eagle owl (*Bubo africanus*), the eagle owl (*Bubo bubo*) and the tawny owl (*Strix aluco*). The alterations produced by these predators are similar, and it is difficult to distinguish small mammal assemblages made by either bird of prey from those of the other. Further, the percentage of postdepositional breakage (fallen rocks, sediment compaction) is very high in all the sublevels and has obscured the original predator-induced breakage patterns and representation percentages of bones. This could be responsible for the fact that the representation profiles do not match the proposed predators (Fig. 3).

Nevertheless, in current assemblages, small differences can only be seen in the intensity of alteration (especially in fractures and digestion, which are slightly higher in the tawny owl) or the overall size of the prey consumed (which is usually greater in the eagle owl) (Andrews, 1990). First, the degrees of digestion observed in the remains from TE9c and TE9a are higher than expected in remains

consumed by an spotted eagle owl (reaching moderate degrees in molars) and eagle owl (reaching heavy degrees in incisors) (Table 6), suggesting that these accumulations are formed by the tawny owl. Secondly, in concentrations with the eagle owl it is common to see skeletal elements belonging to Leporidae, weasels and small herbivores (Andrews, 1990; König et al., 1999; Mikkola, 1983). In sublevels TE9c and TE9a there are abundant leporid remains. These leporids show a good representation of all the skeletal elements and generally have low fracture levels (Huguet, 2007). Furthermore, some of these elements, mainly limbs, have been found in anatomical connection (Huguet, 2007). Taphonomic studies of these taxa have not identified surface modifications caused by consumption by predators, such as bites, pecks or digestion marks (Huguet, 2007). Therefore, it is possible to rule out the intervention of an eagle owl on these remains, since one would expect a greater presence of diaphyseal cylinders, peck marks and epiphyses with light or moderate signs of digestion (Andrews, 1990). All this seems to indicate that within predator category 2, the likely predator is the tawny owl. Besides this raptor, the intervention of *Beremendia fissidens*

Table 5

Breakage of small mammal elements. Results in %.

Tableau 5

Fragmentation d'éléments de petits mammifères. Résultats en %.

Element Breakage	TE9		
	TE9c	TE9b	TE9a
Maxilla			
Complete	0	0	0
With zygomatic arch	0		
Incisors missing	99.4	99	100
Molars missing	97.9	94.7	96.1
Mandible			
Complete	0.8	1.2	1
Inferior border broken	62.6	74.3	64.8
Incisors missing	68	76	73
Molars missing	82.3	69.5	72.5
Teeth			
Incisors broken in situ	3.7	11.3	6.7
Isolated incisors broken	28.5	26	35.2
Total incisors broken	32.2	37.3	41.9
Molars broken in situ	0	0.9	0.9
Isolated molars broken	1	2.5	1.4
Total molars broken	1	3.4	2.3
Humerus			
Complete	6.2	7.1	4.4
Proximal	4.7	7.1	5.1
Shaft	8.5	1.9	3.6
Distal	14.7	18.2	21.2
Ulna			
Complete	0	1.9	1.5
Proximal	5.4	3.2	2.2
Shaft	3.9	6.5	5.8
Distal	0.8	1.3	2.2
Femur			
Complete	2.3	1.3	2.2
Proximal	23.3	13.6	13.1
Shaft	7.8	7.8	2.9
Distal	3.1	10.4	5.8
Tibia			
Complete	0	0	0
Proximal	4.7	7.1	6.6
Shaft	10.1	4.5	8.8
Distal	4.7	7.8	14.6

(Early Pleistocene fossil shrew) as a sporadic predator on a mole (*Talpa cf. europaea*) humerus was also shown in TE9a (Bennàsar et al., 2015).

By contrast, the degrees of alteration in sublevel TE9b do not correspond to those produced by any known predator. Thirty seven percent of the incisors show signs of digestion, which would indicate a nocturnal raptor and certain viverrids as the authors of the assemblage. However, this digestion attains extreme levels of alteration, often associated with predation by diurnal raptors. Furthermore, and despite having a lower average of relative abundance of the skeletal elements, the assemblage from TE9b shows slightly lower percentages of fracture and tooth loss than those from TE9c and TE9a, where a nocturnal raptor has been identified as the author.

For this assemblage two possible hypotheses may thus be put forward: 1) It could be a predator of an intermediate category with an unusually high degree of digestion,

Table 6

Cranial and postcranial digestion of the small mammals of the TE9 sub-levels.

Tableau 6

Digestion crânienne et postcrânienne des petits mammifères des sous-niveaux de TE9.

Element digestions	TE9		
	TE9c	TE9b	TE9a
Incisors			
Absent	72.6	62.9	56.1
Light	23.4	33.9	39.7
Moderate	3.4	1.6	2.7
Heavy	0.6	1.1	1.5
Extreme	0	0.5	0
Molars			
Absent	91.2	91.9	92.7
Light	7.8	7.3	6.6
Moderate	1	0.8	0.7
Heavy	0	0	0
Extreme	0	0	0
Postcranial			
Absent	50	54.7	61.8
Light	48.5	43.9	38.2
Moderate	1.5	1.4	0
Heavy	0	0	0
Extreme	0	0	0

or 2) it could be a mixture of predators. In the first case, it should be noted that several factors are involved during digestion, leading to variability in the alterations produced by different predators, both at the species and the individual level. One of these variables is the pH and enzyme level of the predator (Smith and Richmond, 1972). The pH is more acidic before eating and when the predator has gone for a long period without eating any prey (Duke et al., 1975). This factor, along with the time spent in the stomach, can produce more or less aggressive effects on the remains of small mammal concentrations (Chitty, 1938). Furthermore, the pH is increased in young predators (Andrews, 1990. Raczynski and Reprecht, 1974). Other factors that determine the degree of alteration are the position of the remains in the stomach and the existence of hair and feathers enveloping the skeletal remains for regurgitation, etc. (Andrews, 1990).

Table 7

Postdepositional agents of modification in sublevels TE9 of the Sima del Elefante site.

Tableau 7

Agents de modification postdépositionnelle dans les sous-niveaux TE9 du site de Sima del Elefante.

Postdepositional agents alterations	TE9		
	TE9c	TE9b	TE9a
Abrasion	7.8	20	3
Chemical corrosion	1.2	0.2	–
Concretions	3.9	1.3	0.9
Dissolution	–	0.06	0.3
Manganese oxide	41.8	48.5	43.9
Root grooves	–	–	0.3
Weathering	–	0.2	–

The possibility of a mixture of predators should also be taken into consideration. The mixture of the assemblages contributed by various predators can take place either during the production of the pellets/depositions (that is, there are depositions from several predators in one place before burial) or during fossilization. This sublevel has not revealed any sedimentological, chronological or faunal changes that might suggest the presence of linear changes or overlaps, or any alteration that might indicate that the mixture was produced by a reelaboration of the elements, thus ruling out the possibility that the mixture is postdepositional in origin.

A previous experiment where current assemblages of known predators were mixed (Bennàsar, 2010) has suggested that mixtures can be detected when there is a majority predator in them (one that provides about 70% of the remains in the assemblage), and in some cases, it is possible to identify the species in question. According to this study, one of the main diagnostic parameters for identifying these associations is the presence of discrepancies between the degree of digestion of the incisors, molars and postcranial elements. Moreover, this disparity can also be observed in the levels of general alteration of representation and fracture. However, it should be borne in mind that in archaeo-paleontological assemblages these parameters can be modified by fossil-diagenetic agents.

In the fossils from TE9b, the degree of digestion presented by the molars, postcranial elements and, above all, the incisors shows discrepancies, which would support the hypothesis of a mixture of predators. Within this possible mixture, on the basis of the main alterations observed, a category 2 predator would be identified as the principal agent, probably the same predator as in sublevels TE9c and TE9a (tawny owl). In addition to this predator, there may be the sporadic presence of a predator with higher degrees of alteration or a category 3 predator, reflected in the low representation and in the extreme digestion present in the incisors, although it would not be possible to specify the species to which it belongs.

Thus, the predator responsible for the accumulation of remains from TE9c and TE9a is the tawny owl (*Strix aluco*), which is possibly also the main predator of TE9b (Table 8). This small bird of prey with opportunistic, nocturnal habits includes rodents, voles, shrews, dormice, small birds and insects in its diet. They are strongly territorial and sedentary birds. They nest on rocky walls or in tree hollows, using pellets for quilting eggs. As regards their preferential habitat, they opt for semi-open forests, generally of leafy, deciduous trees and mixed with clearings. They are also common in riverside forests, open landscapes near forests,

and in rocky areas with scattered trees and bushes (König et al., 1999; Lipej and Gjerkes, 1996; López-Gordo, 1974; Mikkola, 1983; Southern and Lowe, 1968). We can thus infer a landscape with semi-open riverside forests with nearby open areas in the Sierra de Atapuerca during the formation of TE9.

These data are consistent with those provided by the taxonomy and analysis of the diversity of the small mammals, herpetofauna, avifauna and macromammals. The paleoecological studies undertaken to date on the basis of rodent and insectivore taxa suggest the existence of a fluvial or lacustrine landscape and a succession of warm and cold climatic events (Cuenca-Bescós and García, 2007; Cuenca-Bescós and Rofes, 2004; Cuenca-Bescós et al., 2004, 2013; Rofes and Cuenca-Bescós, 2006, 2013). In addition, archaeobotanic and faunal results indicate the nearby presence of meadows, possibly humid, semi-open or open, and of semi-open forests (Rodríguez et al., 2011; Rosas et al., 2001, 2006). The area near the Sierra de Atapuerca from 1.2–1.3 Ma thus presented a biome consisting of semi-open riverside forests, or large areas of more or less permanent water, with open meadows nearby (Blain et al., 2010). The climate would probably have been mainly temperate (Rodríguez et al., 2011).

As noted, the predators identified in TE9c and TE9a are opportunistic, and the species found in their depositions are a reflection of the community alive at that time, given that the predator is limited only by the size of the prey and its availability (Table 8). Thus, paleoecological interpretations based on the relative abundances of the small mammal taxa are a good reflection of the hunting habitat of the predators that consumed them. However, the mixture of predators alluded to in TE9b does not allow for this sort of inference.

The microenvironmental characteristics of unit TE9 have been identified through the postdepositional alterations observed in the fossils. These indicate similar conditions for the entire sequence studied. Thus, all the sublevels have been found to show manganese oxide depositions, abrasion, cracking and concretions, although with varying degrees of modification. Other alterations such as dissolution, grooves produced by roots, desquamation weathering and chemical corrosion exhibit a sporadic and uneven presence in the sublevels.

Most of the alterations found are closely related to the microenvironment of the cave, characterized by the low presence of light and by high humidity. These cave conditions are also evidenced by the non-pollen palynomorphs, mainly algae and fungi, which are present above all in TE9 (Rodríguez et al., 2011).

Table 8

Predators identified in this work for each of the sublevels studied and their mode of predation and preferential habitat.

Tableau 8

Prédateurs identifiés dans ce travail pour chacun des sous-niveaux étudiés et leurs mode de prédation et habitat préférentiel.

Predators			
Level	Predators	Predation mode	Habitat
<i>TE9</i>			
TE9a	Tawny owl	Opportunistic	Various semi-forests and riparian forests.
TE9b	Mix? probably Tawny owl + pred. cat. 3	?	? Semi-open forests and riparian
TE9c	Tawny owl	Opportunistic	It is common in various semi-forests and riparian forests.

As regards the production of the remains, the alterations identified indicate that they are resedimented. Although the tawny owl can nest or rest on rocks and rocky soils, in shelters or small blastings (Andrews, 1990; Mikkola, 1983), the alterations shown by some remains (e.g. the abrasion and weathering) indicate that they were not produced in the cave, but were subject to a process of transport from the initial place of deposition located at one of the entrances to the cave.

Such transport may be produced by various mechanical processes, although the abrasion present in all the sublevels of TE9 indicates a predominance of mechanisms associated with water. In TE9c and TE9a, rounding by abrasion affects a small percentage of the remains and generally appears only in isolated cases among the remains, while in TE9b this alteration is more abundant and is sometimes linked to polished surfaces. Such modifications are not abundant or common in small mammals. Although it has been established experimentally that the lower degree of abrasion would occur with silt and clay or fine sand in suspension on fresh bones for a short period of time (Fernández-Jalvo and Andrews, 2003), the suspended-load transport of the remains might not make any alterations. In addition, for this type of transport one should also take into account the partial or total organic covering of the remains at the time of transport and the degree of cohesion of the pellets, because these factors would influence the presence and degree of modification. Thus, the presence of all the skeletal remains in the samples from Sima del Elefante, including the smaller ones, could be associated with the entry of more or less cohesive pellets, and only the remains that were exposed to the erosive particles would present alterations caused by abrasion. The scarcity of postdepositional changes, such as weathering and root grooves, corroborates this hypothesis.

The existence of humid environments at different times during fossilization is evidenced by the intense bacteria and fungi activity observed (Courty et al., 1989; Dorn and Oberlander, 1981; Marín-Arroyo et al., 2008, 2014). Manganese oxide depositions appear on the small mammals in all the sublevels, and are also observed on the surface of the fossil macrovertebrates from Sima del Elefante (Huguet, 2007), suggesting further that the fossilization process of both types of remains occurred in the same microenvironmental conditions. Some fossils exhibit cracking, dissolutions, and concretions, indicating a humid environment with dripping followed by periods of desiccation and temperature changes. All this suggests that the highly humid endokarstic conditions, possibly with flooding, were not favorable for the development of human occupations inside during the formation of TE9. However, the fact that in TE9c the manganese decreases slightly and the concretions increase indicates a slight reduction in humidity and longer periods of desiccation, during which hominids could have taken advantage of to strengthen their presence in the vicinity of the cave. This increased anthropic presence would explain the decrease in the number of small mammal remains and the MNI in this sublevel (the greater the human presence, the less the presence of birds of prey). This is further supported by the greater number of lithic artifacts recovered in TE9c (de Lombera-Hermida et al., 2015).

5. Conclusions

Our taphonomical study of small mammals indicates that the associations from TE9c and TE9a are the result of predation by the tawny owl (*Strix aluco*). By contrast, the small mammal remains from TE9b may have their origin in a mixture of several predators (including the possible participation of the tawny owl and a category 3 predator). These raptors have opportunistic habits, so their concentrations can be considered a reflection of the representation of the species present in the ecosystem. This facilitates paleoecological interpretations based on the relative abundance of the small mammal taxa of TE9c and TE9a.

Our identification of the predator suggests that during the formation of TE9 (1.2–1.3 Ma) the area near the Sierra de Atapuerca had a biome consisting of semi-open riverside forest or large areas of more or less permanent water, with open meadows nearby.

The origin of the remains is mainly exokarstic, and transport into the cave was carried out by various mechanisms of a hydrological nature when the pellets still contained organic matter that covered the remains. The endokarstic environment during the formation of unit TE9 is characterized by high humidity and ponding, preventing the occupation of the cave by the hominids that lived in the vicinity of the Sierra de Atapuerca. Nevertheless, it has been observed that these endokarstic conditions became slightly less harsh in TE9c, which favored their increased presence in the area near the cave.

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